Dendrochronologia 48 (2018) 1–9

Contents lists available at ScienceDirect

Dendrochronologia

journal homepage: www.elsevier.com/locate/dendro

Seasonality matters—The effects of past and projected seasonal climate change on the growth of native and exotic conifer species in Central Europe

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ARTICLE INFO

Keywords:
Abies alba
Central Europe
Climate change
Dendroecology
Forest management
Picea abies
Pseudotsuga menziesii

ABSTRACT

Norway spruce is one of the economically most important tree species in Central European forestry. However, its high susceptibility to droughts poses a strong challenge to its cultivation under future conditions with likely more frequent and prolonged droughts and shifts in the seasonal climate. To compensate for expected losses of forest areas suitable for the cultivation of spruce, more drought-tolerant species are required. Silver fir and Douglas fir are two potential candidates, which promise lower drought susceptibility and equal or even higher yield when compared to Norway spruce.

Using the Black Forest as a regional case study, we assessed the effects of seasonal climate change, including drought stress, on tree-ring width formation of these three economically relevant conifer species over the last 60 years. In addition, we projected potential species-specific growth changes under different climate change scenarios until 2100.

Our results suggest that both silver fir and Douglas fir will possibly experience growth increases in a warmer future climate, as predicted under the 4.5 and 8.5 Representative Concentration Pathway (RCP) climate change scenarios, whereas growth of spruce is expected to decline. Moreover, drought susceptibility in silver fir and Douglas fir is lower than in spruce, as shown for past drought events, and their ability to benefit from milder winters and springs could play a major role in their capacity to compensate for drier summers in the near to mid-term future. This study highlights the need to advance our understanding of the processes that drive drought resistance and resilience in tree species to guide management strategies in the face of climate change.

1. Introduction

Climate change, with an increasing incidence of extreme events and changes in temperature and precipitation patterns, is posing new challenges for forest management (IPCC, 2014a). Droughts have been predicted to become more frequent, as summers are becoming increasingly warmer and drier, with shifts in seasonality of precipitation (Easterling, 2000). In southern Europe, summer droughts have already doubled in intensity and length over recent decades (EEA, 2012), resulting in growth depressions and increased mortality rates of numerous tree species (Allen et al., 2010; Ciais et al., 2005). Changes are also occurring in seemingly healthy forests (Köhl et al., 2010), which could substantially change species-specific growth potentials and stand composition. To mitigate the effect of changes in climatic patterns on forest ecosystems, there is an urgent need for adaptation strategies to maintain sustainable timber production and important ecosystem services like carbon storage (Albert et al., 2015; Field et al., 2012).

Climatic tolerance of tree species and their resilience to extreme events, such as droughts, are two of the main variables used to assess forest vitality (Bolte et al., 2009; Linder, 2000; Lindner et al., 2010). However, our understanding of the processes that drive species-specific responses to seasonal climate and drought events is still limited. To comprehend biological responses to environmental variability, tree rings have been increasingly used as proxies to assess the effect of climate variables (Fritts, 1976). The annual resolution of tree rings allows for the assessment of the direct effect of stress and disturbances on tree growth, often recorded as narrow rings in the case of droughts (Fritts, 1976). Drought effects have been widely studied and response-indices have been proven to provide important insights into the capability of species to cope with extreme events (Lloret et al., 2011). Moreover, the inclusion of intra-annual climate variability and measures of climate extremes are fundamental to correct for over- or under-predictions of

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https://doi.org/10.1016/j.dendro.2018.01.001
Received 23 July 2017; Received in revised form 2 January 2018; Accepted 6 January 2018
Available online 10 January 2018
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models which are often based solely on values of annual mean temperature and precipitation (Zimmermann et al., 2009).

Here, we focus on the potential impacts of climate on growth in one of Europe's economically most important, yet highly drought-sensitive tree species, Norway spruce (*Picea abies)* (Boden et al., 2014; Lebourgeois et al., 2010; van der Maaten-Theunissen et al., 2013). The susceptibility of spruce to drought and associated distributional range shifts could result in major economic losses in Baden-Württemberg, where spruce accounts currently for 41% of the total forest cover (BWI, 2014; Hanewinkel et al., 2012; Hanewinkel et al., 2010). For this reason, we consider two possible substitute conifer species: the native silver fir (*Abies alba)*, and the exotic yet highly productive Douglas fir *(Pseudotsuga menziesii)*. Both species have been seen to be more resistant and resilient to extreme droughts than Norway spruce (Bouriaud and Popa, 2009; Desplanque et al., 1999; Nothdurft et al., 2012; van der Maaten-Theunissen et al., 2013). The reactions of these three conifer species in relation to two of the major drought years recorded in southwest Germany (2003 and 1976) confirmed the higher resilience of silver fir and Douglas fir compared to Norway spruce (Vitali et al., 2017). However, lower resistance and resilience was recorded for all species in relation to the 2003 drought when compared to the drought of 1976, possibly due to the timing of the drought. Even though these two drought events showed a similar intensity when quantified on the basis of annual values of precipitation and temperature used in a drought index, their monthly water balance indicated a stronger deficit for 2003 (Kohler et al., 2010). Hence, drought sensitivity of different tree species may also depend on the seasonality of drought conditions. This aspect has so far received little attention in comparisons of drought tolerance in different tree species.

Here, our aim is to provide insight into the effect of seasonality, defined as patterns of temperature and precipitation (e.g. cold wet winters, or dry hot summers), on annual radial growth of Douglas fir, Norway spruce and silver fir through climate-growth correlations. To ensure that results can be extrapolated to the regional populations of these species, tree cores for each species were collected along three elevational gradients in the southern, central and northern Black Forest.

To assess the future climate suitability of these species in the next century, we projected potential tree-ring growth with the Representative Concentration Pathway (RCP) 4.5 and 8.5 scenarios for this region (IPCC, 2013). More specifically, we address the three following hypotheses:

1) The influence of seasonality of temperature and precipitation on radial growth differs among Norway spruce (*P. abies)*, silver fir (*A. alba)* and Douglas fir (*P. menziesii)*
2) Species reactions to drought events are dependent on species-specific responses to seasonality
3) Future tree-ring growth of Norway spruce (*P. abies)* in the Black Forest will be more strongly affected by climate change than that of silver fir (*A. alba)* and Douglas fir (*P. menziesii)*

2. Materials and methods

2.1. Study sites

For the purpose of this study, we used the same tree cores that formed the basis of the analysis presented by Vitali et al. (2017). They were collected in forest stands from three elevational transects at the western sloped of the northern, central and southern Black Forest. Each transect comprised stands at lower (300–550 m a.s.l.), mid (600–800 m a.s.l.), and higher elevations (900–1200 m a.s.l.). At each elevational range, stands were sampled in northerly and southerly exposition. This yielded a total of 18 sampled sites (Fig. 1, Table S.1, Supplementary map data) and this design was retained for the climate-correlation analysis. The elevational gradients represent decreasing temperatures and increasing precipitation with increasing elevation and hence they permit the analysis of tree growth under substantial climatic variation. Selected sites were representative of conventionally managed and productive forest stands that are typical for the Black forest, whereas extreme dry, shallow or steep sites were not considered. At the date of sampling, the stands were mono-layered and the target trees for coring were selected from dominant or co-dominant positions. All stands were mixtures of the three tree species to allow for a direct comparison of the climatic effect on species growth.

2.2. Tree-ring data

In the spring of 2015, 270 trees per species were sampled for *P. abies*, *A. alba* and *P. menziesii* at the 18 sites. Two increment cores per tree were collected at 1.3 m stem height from two opposite directions, perpendicular to the slope direction to minimise potential bias from reaction wood. Only healthy, dominant or co-dominant trees were cored to minimise the effect of management release effects and competition (Cook and Kairiukstis, 1992). All increment cores were dried and sanded to optimise visibility of rings (Schweingruber, 1988). The WinDendro software (Regents Instruments, Quebec) was used to measure tree-ring widths and create single mean chronologies for each tree. Consequently tree-ring chronologies were built at the tree level and mean chronologies were calculated for the elevational ranges and at the regional level (Fig. S.2). The series-wise correlation function in the dplR package (Bunn, 2010), Gleichläufigkeit and EPS "expressed population signal" (Table S.2) were calculated to estimate the quality of correlations between chronologies, and visual cross-dating was used for data quality control (Schweingruber, 2007, 1988). The common period for all three species was identified between 1960 and 2014, which also coincided with the availability of the interpolated climate data for this region. To carry out the climate-correlation analysis, the tree-ring series were detrended (TRI) using cubic smoothing splines (fit with 50% frequency cut-off ($p = 0.5$) at 60 years) to minimise the effects of age differences, and further pre-whitened by autoregressive modelling (Cook and Kairiukstis, 1992). To compare the effects of drought events between the species and elevational ranges, the mean regional chronology for each species and altitude was subtracted from the single trees' chronologies to accentuate the climate dependent growth while retaining the absolute differences between altitudes and species.

2.3. Climate data and drought years

Monthly and site-specific precipitation and temperature data were retrieved from the nationwide interpolated data produced by the REGNIE project and distributed by the Deutscher Wetterdienst (2013) for the 1960–2014 time series. The "drought aridity index" DMI (De Martonne Index) was adapted from Maliva and Missimer (2012), to produce a monthly and annual aridity index for each site and season. In our case, a DMI of 3 was the minimum calculated for extreme drought years, and the lower the DMI value the dryer the season (Fig. S.1). Seasons were defined by 3 calendar months (i.e. spring = Mar.–May, summer = June–Aug., autumn = Sept.–Nov., winter = previous year Dec- current year Feb.).

To assess the effect of extreme drought years, we focused on the events of 2003 and 1976, which showed an average DMI of ~3 and corresponded with strong growth reductions in all three species (see also Vitali et al. (2017)). However, we expanded the selection to include the less intense droughts (i.e. Mar.–Aug. DMI < 5, years:1974, 1990, 1991, 1993, 2011, Fig. S.1). In addition, the mean DMI for spring and summer was calculated separately for each dry year and we could discern two main typologies depending on the drier of the two seasons: spring droughts (spring drier than summer), and summer droughts (vice-versa).

The climate projection data were retrieved from the Royal Dutch Meteorological Institute KNMI climate explorer website (climexp.knmi.nl), which allows the export of the PCC WG1 AR5 "Atlas" results (IPCC, 2013). The spatial resolution of the projection models is a

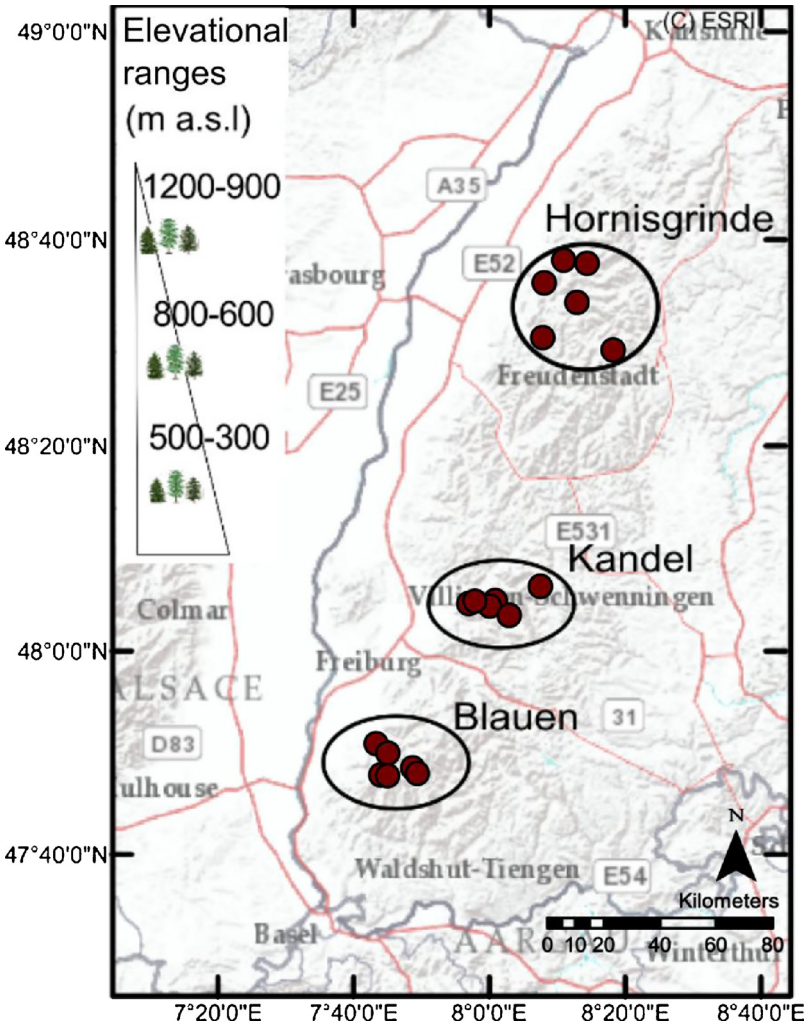

Fig. 1. Locations of study sites in three main transects on the westerns slopes of the Black Forest mountains Hornisgrinde, Kandel, and Blauen. The elevational transect is subdivided into three elevational ranges at which stands in both northerly and southerly expositions were sampled.

half degree latitude (Wayne, 2013), which did not allow differentiation between the single sites and elevations sampled in our study. Therefore, precipitation and temperature projections were considered at the regional level (Fig. S.3). To address the uncertainties of climate change projections, different greenhouse gas emission scenarios have been considered. The RCP 8.5 (highest radiation forcing scenario) and the RCP 4.5 (lowest probable scenario) were selected to analyse the effects of the scenarios with the strongest and least changes in temperature and precipitation between 2017 and 2100. To assess trends in seasonal patterns, the models for the RCP 4.5 and 8.5 were retrieved from the Monthly CMIP5 scenario runs on the KNMI website (Fig. 2, Fig. S.4).

2.4. Growth-climate response analysis

The detrended tree-ring chronologies and climate data were summarised according to elevational levels and used to perform a running window correlation function with the treeclim package (Zang and Biondi, 2015). Calculations were performed for all seasons (3-months averages) with a 30-year moving window from 1961 to 2014. Monthly climate correlations were calculated considering the months from June of the previous year to September of the current year. Analyses of variance (ANOVA) and Tukey's PostHoc test were used to assess differences between the drought years.

A linear regression equation was developed from the relationship between the independent variable DMI separately calculated for the 4 seasons for the time period 1960–2014 and raw tree-ring chronologies as the dependent variable ($TRW \sim DMI_{summer} + DMI_{spring} + DMI_{winter} + DMI_{autumn}$). A forward step-wise selection process was carried out with the regsubset function (Lumley and Miller, 2009). Although spring- and winter-DMIs showed collinearity with an $r^2 \sim 0.5$, all 4 seasons were included in the final model, as in one case (the Norway spruce model) the inclusion of spring-DMI improved the model fit, while it did not modify the results of the other species models results. The same model was used for all three species to allow for a comparison of the between-species trends. Interactions between the predictors were tested and subsequently discarded as not significant. The DMI was considered a good proxy as it showed a strong linear correlation with total precipitation ($r^2 = 0.97$) and temperature means ($r^2 = 0.57$). To estimate the species' growth behaviour under projected climate change, the projected seasonal DMI was calculated for a 10-year time-windows at the turn of each decade (e.g. 2016–2025 average for the decade of 2020), for the averages of the 8.5 and 4.5 RCP scenarios and for the average of all scenarios. To calculate the change in growth we considered the mean values of tree rings for the common period as growth baseline. Therefore, the predictions show the relative growth projection compared to the average growth over the last 50 years for each species in the Black Forest. All computations were performed in the 3.4.2 R version (R Core Team, 2017).

3. Results

3.1. Growth correlations with seasonal climate

The climate-correlation analysis showed that summer precipitation at low elevations was significantly positively correlated with tree-ring

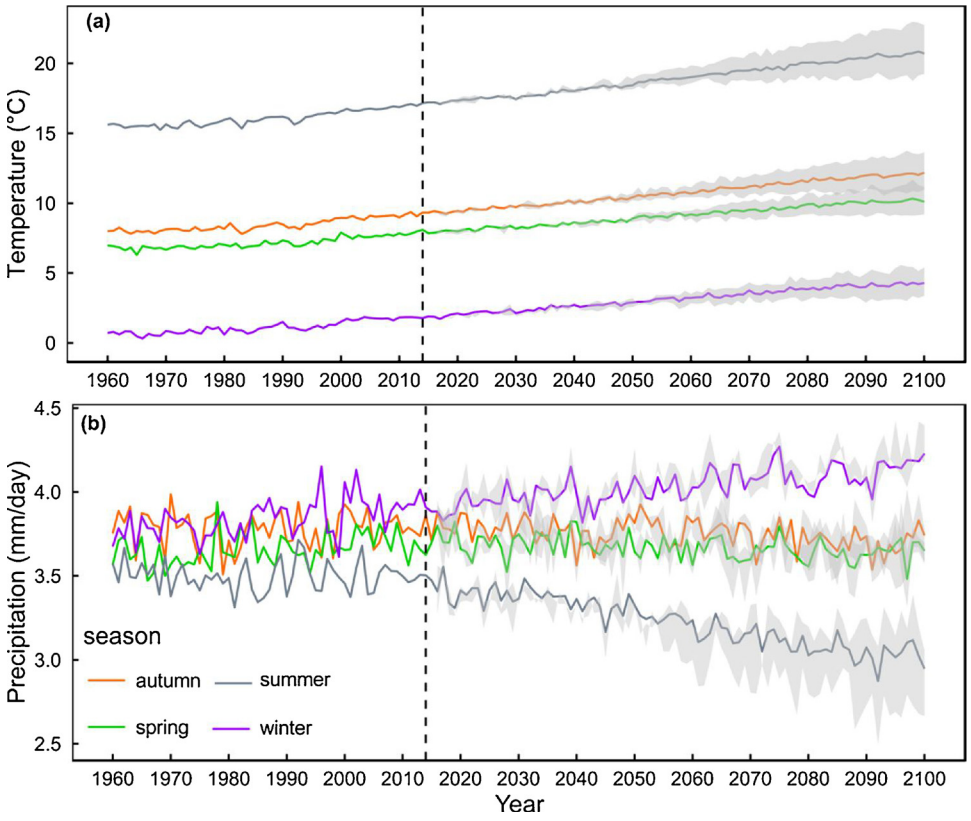

Fig. 2. a, b Seasonal averages of model runs (RCP 4.5 and 8.5) for temperature and precipitation. Variance expresses the mean projections for the single scenarios, where RCP 8.5 forecasts the highest variance boundary for temperature and the lowest for precipitation, respectively, and RCP 4.5 produces the lowest temperature variance boundary and the highest precipitation.

growth for all three species (Fig. 3e). Douglas fir and Norway spruce also showed significantly positive effects of summer precipitation on tree-ring growth in mid-elevation forests (Fig. 3c). Summer temperature had a strong negative influence on tree-ring width (Fig. 3b, d, f). At low elevations, high summer temperature affected both Norway spruce and Douglas fir negatively, but not silver fir (Fig. 3f). In addition, Norway spruce showed negative correlations with summer temperature at all elevations, whereas the strength of correlations between summer temperature and tree-ring width in Douglas fir and silver fir declined with increasing altitude (Fig. 3b, d). Silver fir and Douglas fir growth was positively correlated with winter and spring temperature especially at high and mid elevations (Fig. 3b, d).

Correlations between tree-ring widths and precipitation and temperature appear to have been consistent over the last 50 years. The only evident fluctuations (correlation coefficients crossing from negative to positive values or vice versa) were observed for autumn temperature values after the year 2000; this shift from a positive to a negative correlation is recognizable across altitudes for all species.

Congruent results emerged from the monthly correlation coefficients, showing the high positive effect of higher June precipitation for all species, especially at mid and low elevations, and for Douglas fir also at high elevations (Table 1). Silver fir growth was also strongly positively correlated with precipitation in September of the year preceding the tree-ring formation (previous year). The previous year temperature had a negative impact on growth of Norway spruce (July, September and December). June temperature of the current year had a negative effect on Douglas fir growth at low altitudes, while silver fir did not show any negative correlation with temperature. Winter and spring temperature correlations with tree-ring width differed between the species and altitudes, showing however, no consistent pattern (Table 1).

3.2. Drought years

The 2003 and 1976 drought years had a pronounced negative influence on tree growth in the region (Kahle et al., 2008; van der Maaten-Theunissen et al., 2013; Zang et al., 2014), while the less extreme dry years (i.e. 1974, 1990, 1991, 1993, 2011; Fig. S.1), showed different degrees of responses. According to these categories, 1976 may be considered an early drought, commencing in March and extending into summer, since the summer months were as dry as the spring months. In contrast, the 2003 drought started only in June.

The 1976 and 2003 droughts were not significantly different in terms of the annual DMI. While the summer was much drier in 2003, both spring and summer were arid in 1976. Moreover, the soils in the spring of 1976 were reported to be also especially dry following a dry winter (Eckstein et al., 1984). All three tree species showed a significant reduction in radial growth in these years at all elevations (Fig. 4). Responses to the less intense droughts were less consistent across the species. Summer droughts affected tree-ring growth significantly, whereas spring droughts did not have a significant influence. For example, the very dry spring in 2011 had a negative effect on spruce at mid and high elevation only, whereas the other species were not affected. Similarly, in the years 1990 and 1993, which had drier springs than summers, growth decreased only at low elevations. In contrast, summer droughts had a more consistently negative effect on growth in all species, in particular when the DMI was below 5 for both seasons, spring and summer, of the respective year.

3.3. Tree-ring growth projections

Average tree-ring widths were modelled for Norway spruce, silver fir and Douglas fir for the Black Forest region to assess possible growth trends until the end of this century (Fig. 5, Table S. 3). The linear model accounted only for the effect of the aridity index of the four seasons, therefore these trends should be considered in light of this limitation. Silver fir and Douglas fir showed a positive growth trend under both climate scenarios, with a projected increase in tree-ring width of 0.35 mm for the former, and 0.15 mm for the

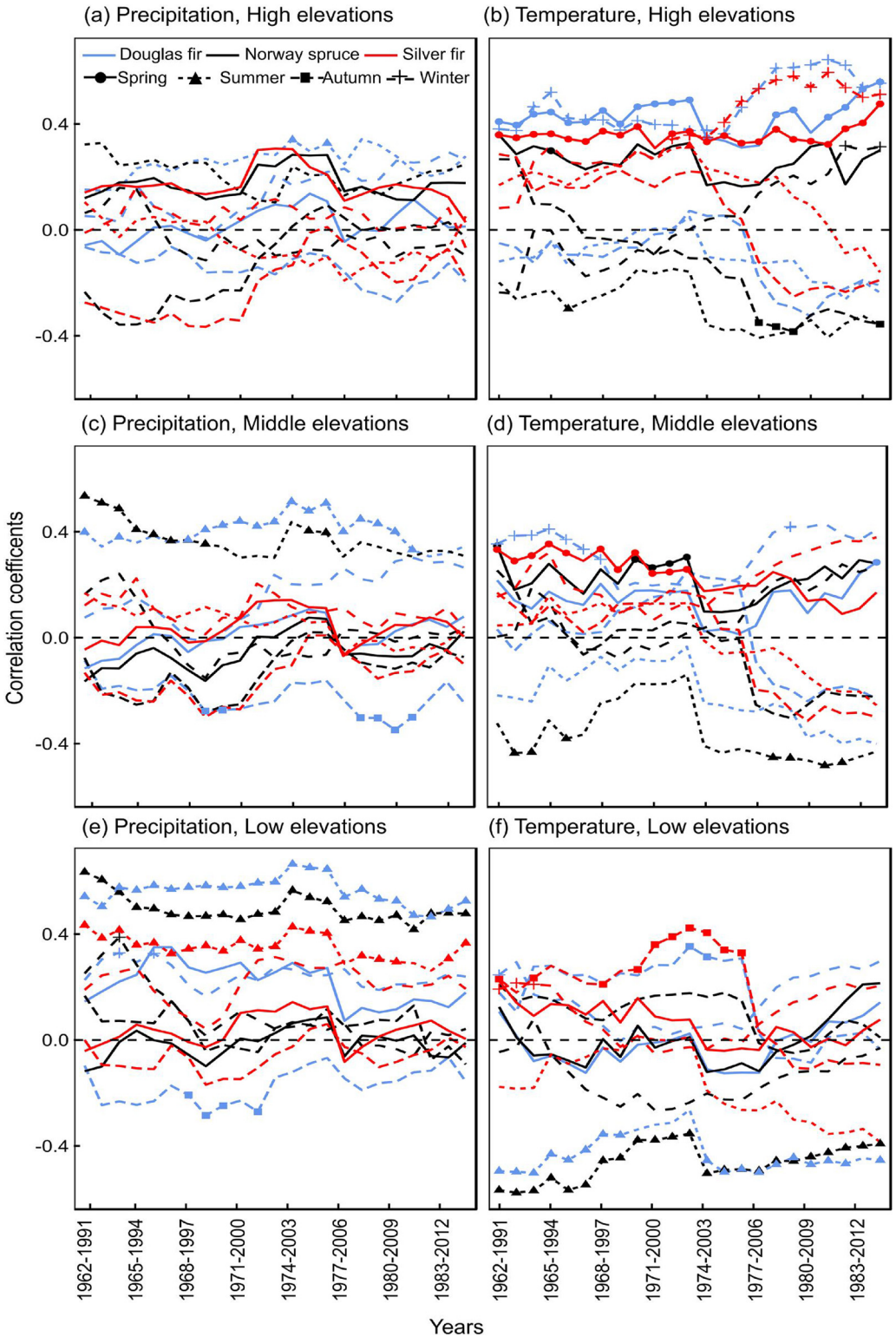

Fig. 3. Correlation coefficients between the tree-ring chronologies of Douglas fir, Norway spruce, and silver fir, for the three elevational ranges, and the seasonal temperature and precipitation, for years 1960–2014, with a 30-year moving window, (lag 1 year). Seasons are calculated as the average of 3 months for temperature and precipitation. The symbols indicate significant correlations ($p < 0.05$).

latter by 2090. Modelled growth based on the two RPC scenarios indicates the same trends. However, the difference between the two scenarios was strongest for silver fir. For Norway spruce, the growth projections cross after 2050, after which the RCP 8.5 shows a stronger negative impact on tree-ring growth, while for silver fir and Douglas fir, growth rates are more favourable throughout under this scenario.

4. Discussion

4.1. Influence of seasonality and altitude on tree-ring growth

Looking at the long-term sensitivity of tree-ring growth as indicated by the correlation analysis (Fig. 3), it appears that summer temperature and precipitation have been driving growth at low elevations for the last 60 years. At low altitudes, tree-ring growth of all species was

Table 1
Significant correlations between tree-ring width and monthly precipitation and temperature for the three elevational ranges (L = low, M = middle, H = high) were calculated from June of the previous year to September of the current year. Months from the previous year are indicated by lower case letters, and months of the current year are indicated by capital letters. Only months with significant correlations are shown.

		Precipitation		Temperature							
		sep	JUN	jul	sep	dec	JAN	FEB	MAR	MAY	JUN
Norway spruce	H			▽ -0.26			▲ 0.22				
	M		▲ 0.29	▽ -0.19							
	L		▲ 0.29		▽ -0.22	▽ -0.21			▲ 0.28		
Douglas fir	H		▲ 0.28						▲ 0.23		
	M		▲ 0.37								
	L		▲ 0.31					▲ 0.23			▽ -0.17
Silver fir	H									▲ 0.28	
	M	▲ 0.26	▲ 0.27				▲ 0.26				
	L	▲ 0.22	▲ 0.35								

positively correlated with summer precipitation, and negatively with summer temperature, confirming observed growth decreases in dry and hot summers (Ciais et al., 2005). Radial growth of Norway spruce and Douglas fir appeared to be influenced by seasonality of temperature and precipitation during the summer months from low to mid elevations. In contrast, radial growth in silver fir at mid and high elevations was not influenced by variation in summer climate. At high elevations the correlations were not significant for all species. The results indicate for the Black Forest region a sensitivity of spruce and Douglas fir to summer precipitation up to 800 m a.s.l., while silver fir was sensitive only up to 400 m a.s.l.

Douglas fir and silver fir also showed strong positive correlations with spring and winter temperature at high elevations. Higher spring temperatures may benefit silver fir growth by reducing the occurrence of late frost, to which it is susceptible (Lebourgeois et al., 2010) or by enhancing the early start of cambial activity (Gričar and Čufar, 2008; Swidrak et al., 2014). Similar results were recorded in Poland, where winter and early spring temperatures were the main factor controlling growth increments (Feliksik and Wilczyński, 2009). The positive correlations with winter temperature (especially January and February), and significance of the winter-DMI in the model, might indicate also a beneficial effect of a lack of deep soil freezing at high elevations (Sutinen et al., 2008), thereby benefitting the winter activities of Douglas fir and silver fir. In fact, under mild winter conditions (~5 °C),

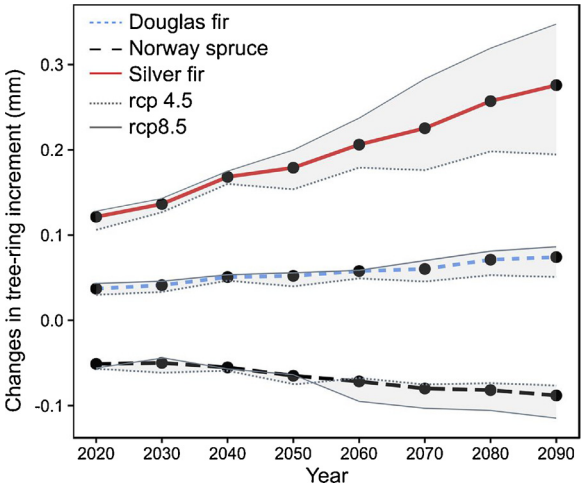

Fig. 5. Projected changes in tree-ring width increment with climate change for the three conifer species relative to the reference period 1960–2014. The RCP 4.5 and 8.5 climate change scenarios were used to calculate the minimal and maximal variation (grey lines); an additional average model between the two scenarios was used to calculate the mean trend lines. A window of ten years was used to calculate the mean projected precipitation and temperature for the indicated decade. The goodness of fit (r^2) of the models was 0.349 for silver fir, 0.06 for Douglas fir, and 0.087 for Norway spruce (Table S.3).

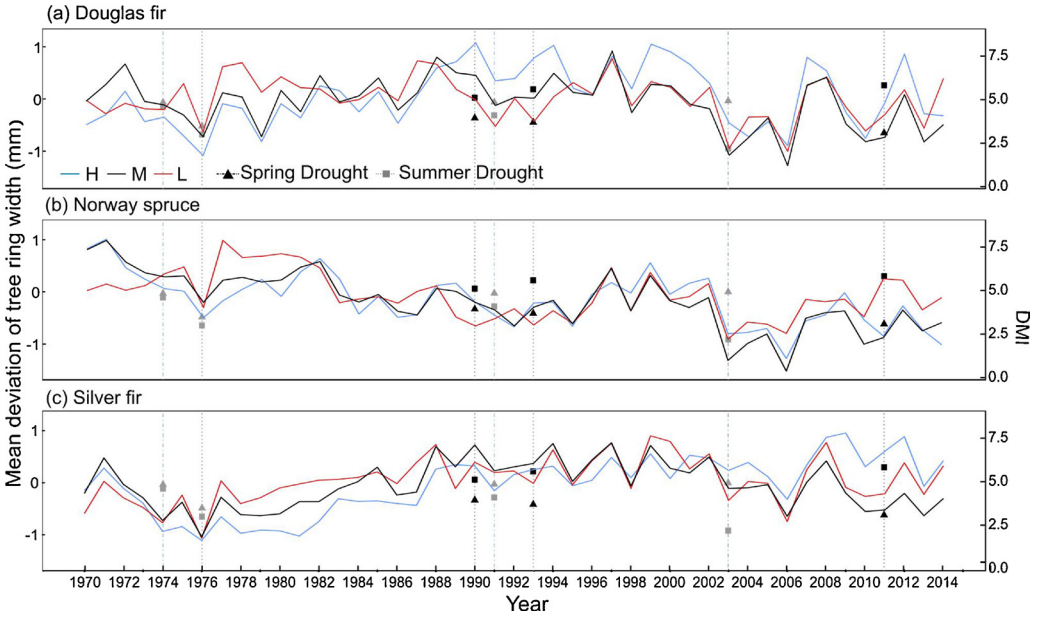

Fig. 4. a, b, c Mean deviation of tree-ring width from average chronologies for the elevational ranges and the tree species between 1979 and 2014. Spring and summer drought indices are indicated for years with a DMI of the growing season (Mar.–Aug.) lower than 5. Triangles represent the DMI for the spring of that year, and quadrats for summer. If the most dry period was in spring, the shapes are colored in black, in gray if summer was the driest period.

photosynthetic activity was recorded for these species (Bailey and Harrington, 2006; Emmingham, 1977), which improved growth and carbohydrate storage in the following year (Guehl et al., 1985; Harrington et al., 2010; Lebourgeois, 2007). Correlations of silver fir growth with precipitation from mid to high elevations were not significant, indicating that temperature and not precipitation is the limiting factor at these elevations (Carrer et al., 2010; Rolland et al., 1999). This response is consistent with silver fir's higher resistance to drought when compared to the other conifers. It shows a drought-avoidance strategy and a high water-use efficiency both in areas with good growing conditions as well as drier sites (Carrer et al., 2012; Peguero-Pina et al., 2007), although its growth in Mediterranean climates has been seen to become constrained by low water availability in spring and summer (Gazol et al., 2015). These findings support our first hypothesis that the three species respond differently to seasonality, although their responses to summer precipitation at low elevations were the same.

Although the significant influences of temperature and precipitation along the elevational gradient suggested a consistent effect for the last 60 years, a sudden change in the future due to the rapid modifications of seasonality patterns driven by climate change should be not ruled out (Anderegg et al., 2015; Barros et al., 2017; Falk and Mellert, 2011; Oleksyn et al., 1998). Owing to the strong effect of summer precipitation and temperature detected by the climate-correlation analysis, extreme summer droughts might be one of the drivers of such swift changes in growth patterns that will influence species' vitality (Williams et al., 2012). The effect of extreme events has been seen to be a major driver of growth reduction also on mesic sites, where neither temperature nor precipitation are limiting factors under normal conditions (Carrer et al., 2012). This was also the case in our study, where growth was shown to be strongly reduced in extreme drought years when both spring and summer were particularly dry (Fig. 4). Whereas spring droughts affected all tree species consistently less and had no effect on radial growth in the following year, summer droughts, particularly the one in 2003, caused a stronger growth reduction, especially in spruce (van der Maaten-Theunissen et al., 2013). Moreover, extreme droughts have proven to affect growth up to 1–2 years after the drought in non-arid environments such our sites (Anderegg et al., 2015). However, several reductions in radial growth were not associated with droughts but caused by other influences. For example, the low growth in 2006 was explained by a region-wide strong mast year that was recorded for all three species (Meining et al., 2013). Nonetheless, summer droughts were confirmed to be one of the strongest drivers of growth reductions. Hence an increase in the frequency of summer droughts such as in 2003 will likely have a negative effect on all three species, with the highest impact on spruce (Vitali et al., 2017). However, a combination of extreme spring-summer drought with a preceding dry winter such as in 1976 (Eckstein et al., 1984), appears to have affected all species equally. These results confirm our second hypothesis that species reactions to drought events are dependent on species-specific responses to seasonality.

4.2. Species-specific growth projections

A positive trend in projected radial growth was found for silver fir and Douglas fir and a negative trend for spruce for all climate scenarios for the next decades. However, given the uncertainties of the climate scenarios, the low statistical strength of the model, and the low EPS of some chronologies, the results need to be interpreted and used with caution (Merow et al., 2014). These results should be considered as a long-term projection of the general direction of growth trends of healthy dominant trees of the different species for this region. It is possible that with further analysis and accounting for mortality rates, the net growth at the population level might be different. For example, single individuals might grow better, but the whole population might show an increase in mortality rates, hence a higher turnover (van Mantgem and Stephenson, 2007).

Nonetheless, these results provide an indication of the different growth responses of the three economically important species in this region. The projected increasing summer temperature and decline in summer precipitation for this region will likely extend the negative effects on tree growth now seen at low elevations to increasingly higher altitudes (Körner, 2007). Hence an increasing proportion of existing Norway spruce forests may be affected by hot and dry summers, and low elevations may become unsuitable for cultivation of Norway spruce (Hanewinkel et al., 2012). The strong correlations with summer temperature and precipitation indicate that all species would show higher growth in relatively cool and moist summers, hence, they will be negatively affected under climate change scenarios indicating drier and hotter summers (IPCC, 2014a). However, at the projected levels of precipitation for high elevations of the Black Forest Douglas fir and silver fir do not appear to be negatively affected by increasing summer temperatures. This may be attributable to their deep root systems (Köstler et al., 1968). It has been observed that uptake of water by Douglas fir in dry summers was from "deep water", accessible through roots at greater soil depths (Thomas et al., 2015).

Regional climate projections also predict warmer winters and springs and an increase in winter precipitation (Fig. 2). This might benefit Douglas fir and silver fir through enhancement of winter photosynthetic activity and shortening of the winter dormancy period (Bailey and Harrington, 2006; Emmingham, 1977). Earlier spring snow melts would also benefit the early cambial activity of the firs, especially at high elevations, where the vegetation period is shortened by long duration of snow cover (Beedlow et al., 2013; Gričar and Čufar, 2008; Hughes et al., 1999; Swidrak et al., 2014). However, it was also suggested that if the required chilling period is not achieved in particularly warm winters, the trend toward earlier budburst could be reversed (Harrington et al., 2010). In addition, reductions in snow cover (height and duration) may reduce soil water availability in late spring and summer, even if the total amount of precipitation would remain the same or increase(Barnett et al., 2005).

Overall, it appears that Norway spruce will experience the most difficulties in coping with future warmer and drier climatic conditions during the growing season. Our results show no improvement for the projected growth of spruce. Together with the potential impact of drought events, this finding supports the outcomes of other studies that have stressed that spruce has a low resistance to drought (Boden et al., 2014; Lebourgeois et al., 2010; van der Maaten-Theunissen et al., 2013; Vitali et al., 2017), and exhibited declining growth rates in the recent past (Yue et al., 2014). In addition, its potential to recover from consecutive drought years may be very low, although no evidence is available for this region, or for Silver fir and Douglas fir.

Annual climate averages only show part of the effect of climate on growth; and the increasing frequency of climate extremes suggests the importance of including their effect on species growth projections (Zimmermann et al., 2009). Although the projected trend for radial growth of spruce showed only a small change (Fig. 5), the impact of extreme events has the potential to drastically reduce its growth. In contrast, Douglas fir and silver fir growth increased and higher resistance and resilience to drought make them suitable candidates for changes in the tree species composition while maintain a desired proportion of conifers in the forests (Aitken et al., 2008; Bonan, 2008; Vitali et al., 2017). Silver fir seems to be the species that will cope best with future conditions, in particular at mid and high elevations. In comparison, Douglas fir does not show such a positive projection, however, owing to its undeniably higher growth rates, it should be considered a strong species to fill gaps in timber production. Considering the average growth and future trends, Douglas fir will still be the fastest growing species of the three (+2% tree-ring width, average TRW 4,5 mm), and silver fir might show a 10% increment (going from an average TRW of 3.0 mm to 3.3 mm).

However, it should be stressed that these results are based only on the analysis of radial increment in healthy trees (survivors) with no

information on mortality rates within populations. Hence, when upscaling to the population level, different outcomes may be observed. In addition, the effect of consecutive drought years on the drought tolerance and recovery potential of these species has not yet been observed in this region. Species may respond quite differently to such a situation of successive droughts, which could become more frequent with climate change (IPCC, 2014b). This may also increase the effects of other abiotic an biotic disturbances like forest fires and pests in areas that were previously scarcely affected (Anderegg et al., 2015; Williams et al., 2010).

4.3. Outlook

This study has shown that although Norway spruce is the most commercially important conifer species in the Black Forest region, it is also the most vulnerable to climate change. Silver fir and Douglas fir are not only more drought resistant; they also appear to be better adapted to projected changes in seasonal climatic conditions such as warmer winters. However, this study was based entirely on dendroecological analyses and no data on mortality rates were considered. Hence any recommendations from this analysis are associated with high uncertainties regarding the future potential of the three tree species under changing conditions of climate, pests and pathogens, and abiotic disturbances. Further research is required on the effect of successive extreme drought years and mortality rates in conventionally managed forests. Moreover, preventive adaptive measures should be in place before the systems reaches a critical level (Aitken et al., 2008; Schelhaas et al., 2015). In this context mixed-species forests may reduce the occurrence of large-scale dieback (Jactel et al., 2017). The required conversion of Norway spruce forests and the expansion of other more drought-tolerant species require a massive effort in forest management.

Acknowledgements

This study was financially supported through a KLIMOPASS grant (no. 4500354096/23) provided by the Baden-Württemberg Ministry of Environment, Climate and Energy to J. Bauhus. U. Büntgen received funding from the Ministry of Education, Youth and Sports of CR within the National Sustainability Program I (NPU I; GN LO1415). The authors thank the generous support of ForstBW, the cooperating forestry districts and competent foresters without whom the project would not have been possible. We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling, which is responsible for CMIP, and we thank the climate modelling groups for producing and making available their model output. Further thanks go to Dr. Rüdiger Unseld for his valuable input in the development of this project, to Thomas Weich, Audrey Louy, Clara Arranz and Raphaële Piché for their support of field work, and Adam Benneter for the support with the modelling.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.dendro.2018.01.001.

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